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ON THE USE OF THE GUILD CONCEPT IN PLANT ECOLOGY

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Abstract: The original definition of the guild is reiterated and the concept discussed and placed in the context of related concepts such as resources and competition. From this conceptual framework the current use of guilds in studies of plant community ecology is evaluated. We discuss the criteria with which species are assigned to guilds, the association of guilds with specific communities, the resource classes on which guilds are based, and the competitive relationships between species of a guild. We conclude that the guild is presently applied in a much more loose way as compared to its original definition. In particular, the a priori assignment of species to guilds on the basis of the use of well-defined resource classes is often relaxed. This obscures the insight that the guild structure may provide in the role of resource partitioning and competition in structuring the community. A more strict use of the concept is advocated.

INTRODUCTION

A central question in plant ecology concerns the causes of the often tremendous species diversity existing within plant communities. Interspecific competition, habitat heterogeneity, stochastic processes (random and localized colonizations and extinctions) and other factors may contribute to this variation. It has been suggested that the analysis of species co-occurrences in discrete geographic localities can provide insight in the importance of competition vs. other factors in ecological communities. This analysis has been performed mainly on co-occurrence data of plant species in small quadrats (PLATT & WEISS 1977, WILSON et al. 1987, WILSON & SYKES 1988, ZOBEL & ZOBEL 1988, KLIMEŠ et al. 1995) and for animal occurrences on islands in archipelagos (GILPIN & DIAMOND 1984, STONE & ROBERTS 1992). Several of these studies perform this analysis of co-occurrences on species belonging to the same guild. Because it is expected that species of the same guild compete more strongly for resources than species of different guilds, the number of species of the same guild that will co-occur on the same location is restricted (WILSON 1989, WILSON & ROXBURGH 1994, LEPŠ 1995). Turning this argument around, it is argued that a constant proportion of the species in each of the guilds (guild proportionality) indicates that intra-guild competition is an important determinant of community composition (but see BARTHA et al. 1995). More co-occurrence than expected by chance would point at the operation of environmental heterogeneity and other factors as structuring forces (LEPŠ 1995).

Whether such analyses of co-occurrences of guild species gives valuable insights in community processes depends on a consistent and unequivocal use of the concepts guilds,

resources and competition. Below we summarize the definitions of these terms from a current textbook and the original literature and discuss their implications for the use of guilds in unravelling the causes of diversity maintenance of plant communities.

BACK TO THE ROOT: SOME DEFINITIONS

Resources

The distribution and abundance of species are generally seen to be controlled by four broad classes of primary factors: conditions, resources, predation (including the effects of herbivory and pathogens in the case of plants) and disturbance. Conditions are defined as abiotic environmental factors, which vary in time and space, to which organisms are differentially responsive (BEGON et al. 1990: 47) and are also termed physico-chemical stress factors (TILMAN 1990). For plants, examples include temperature, soil pH, salinity and vapour pressure deficit. Although conditions can be altered by some organisms, they are not consumed or used up by them. It is in this respect that conditions differ from resources. Resources may be defined as all things that are consumed by organisms, or as quantities that can be reduced by the activity of the organisms (BEGON et al. 1990: 79). Light, carbon-dioxide, water and mineral nutrients are obvious resources for plants (food and energy resources). According to this definition, also pollinating animals, agents responsible for seed dispersal or gaps in the vegetation necessary for successful germination and seed establishment should be regarded as resources: they are quantities that may be available in limited supply and if plants utilize them they are no longer available to other plants. Levels of resources are not only determined by consumption of the individuals of a population themselves, but also by resource utilization by other populations, resulting in resource competition (see below).

The other factors mentioned above (conditions, predation or herbivory, disturbance) may moderate these competitive interactions. Unfavourable conditions reduce plant growth, herbivores and pathogens consume parts of the plant biomass, and disturbances are external factors causing a destruction of (parts of) plants (GRIME 1979, VAN ANDEL & VAN DEN BERGH 1987). Co-occurring plant species may be differentially affected by all of these factors, altering the competitive relationships between species.

Competition

Having used the word competition it is now necessary to define this process within plant communities. Given the profound differences in opinion, an exhaustive treatment of the concept of competition is impossible within the scope of this essay (the botanically interested reader is referred to BRAAKHEKKE 1980, THOMPSON 1987, TILMAN 1987, THOMPSON & GRIME 1988, LAW & WATKINSON 1989, GRACE & TILMAN 1990, GRACE 1995). Some workers use competition to denote all negative interactions between plants, including those in which plant species affect each other by changing the abiotic conditions (e.g. pH). However, for the purpose of the current discussion, we restrict ourselves to competition for resources.

Competition may thus be defined as "the interaction between organisms brought about by a shared requirement for a resource, and leading to a reduction in survivorship, growth and/or reproduction of the organisms" (BEGON et al. 1990: 197). This definition combines two important aspects of resource competition, a proximal aspect stressing the exploitation of a

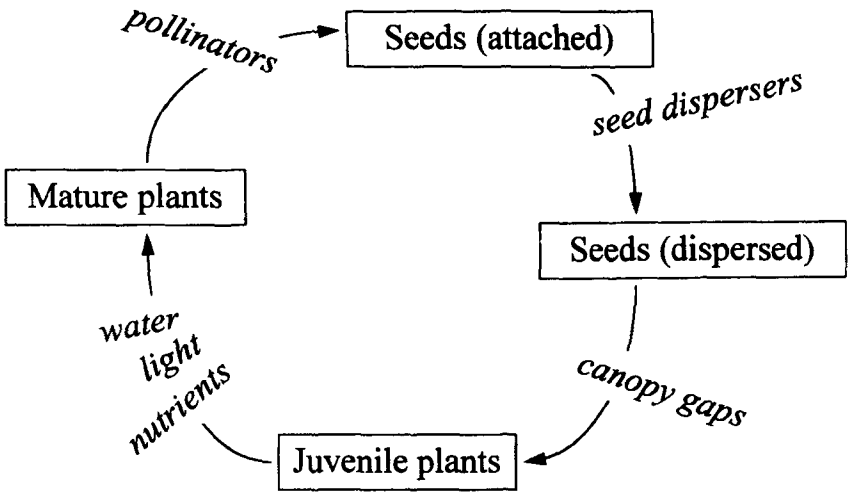

Fig. 1. A highly simplified life cycle of a hypothetical plant species. The arrows indicate the life cycle transitions that together determine the population growth rate. Examples of resources for each of the transitions are given in italics.

common resource that organisms compete for, and an ultimate aspect emphasizing the demographic consequences of competition (GOLDBERG 1990). It should be noted that competition (the ultimate component) is a population phenomenon that has firm ground in the life cycle of the species. Resources affect the demographic transitions as depicted in Fig. 1; competition lowers the resource levels and reduces the population growth rate. Conditions, herbivory and disturbances may modify these relationships.

The guild

The guild is defined as a group of species that exploit the same class of environmental resource in a similar way (ROOT 1967, SIMBERLOFF & DAYAN 1991, see BEGON et al. 1990: 718). It is not always clear what should be considered as a "class of environmental resource" and this is especially true in the case of plants. As all plants use the same food and energy resources, all plant species could arguably be grouped in a single guild. However, resources, as defined above, vary greatly in their nature and may affect a variety of life cycle transitions (Fig. 1). To structure this variation, **resource classes** may be identified, a set of related resources that are measured in similar units such as above- and belowground resources or resources that affect certain life cycle transitions. Examples have been proposed such as badger mounds, on which a subset of prairie species depend (PLATT & WEISS 1977), or bumblebees that pollinate a certain group of flowering plants (PYKE 1982). Similarly, water and nutrients in the soil may be grouped in a class of belowground resources. These resources within resource classes may be termed **resource dimensions** (PLATT & WEISS 1977), such as badger mounds that differ in soil moisture or bumblebees with short and long probosces

that pollinate flowers with short and long corollas. The availabilities of nitrate, ammonium and phosphate may be considered as resource dimensions within the class of soil resources. There is typically a continuum of resource dimensions within the class. The species of a guild utilize the same resource class but may use resources of different dimensions.

As species of a guild depend on the same class of a resource, competition may be expected to be potentially strong within a guild, leading to a reciprocal inhibition of the population growth of each of the species (LAW & WATKINSON 1989, PIANKA 1994: 340). This by no means implies that resource competition within the guild will be strong in present-day communities, for two reasons. First, species of guild may utilize resources of different dimensions, such as a different size or form, from different position in space, or in a different season. The most compelling examples are from the animal literature, such a lizard guilds feeding on termites in which individual species specialize on termites of different size (PIANKA 1969 as cited in WHITTAKER 1975, SIMBERLOFF & DAYAN 1991). For plants, PLATT & WEISS (1977) demonstrated that species occupying gopher mounds show differential resource usage on the basis of their water requirements and dispersal capabilities. Such specialisation in resource use may or may not be the result of competition in the past. Competition within the guild may also be small if the resources of the class that guild species commonly exploit are not the resources that limit the population growth rate of the species. For example, if the bumblebee density is sufficient to pollinate all the flowers of the species of a guild of bumblebee-pollinated species, there is no a priori reason to assume that interspecific competition within the guild will be stronger than between guilds. Intense intra-guild competition is more likely when guilds are based on common use of a class of resources that limits the population growth rate (the resource class affecting the bottle-neck transition in the life cycle of Fig. 1).

Implications

These definitions, and especially the close conceptional links between guilds, competition and resources, have four important implications.

(1) Not every species group is a guild

Based on the original definition of ROOT (1967), a guild should be defined as a group of sympatric species using a similar class of resources (canopy gaps, pollinating insects, seed-dispersing ants, Fig. 1). This definition places restrictions on the criteria on the basis of which guilds are constructed (SIMBERLOFF & DAYAN 1991). Taxonomic relatedness is not a proper criterium (BEGON et al. 1990: 718-719) as closely related species may or may not use the same class of resources. Species classifications based on the level of tolerance to extreme values of conditions (temperature, salinity, pH) are not directly related to common resource use and species with a same temperature preference or salinity tolerance are not a guild. However, in the current plant ecological literature there is a tendency to construct guilds on the basis of a wide variety of shared traits, including preferences (e.g. temperature, pH), growth forms (e.g. leaf anatomy, leaf shape, plant height), family, or a combination of traits referred to as a strategy (VAN DER MAAREL 1988, FERNÁNDEZ-PALACIOS 1992, BOUTIN & KEDDY 1993, KLIMEŠ et al. 1995, O'BRIEN et al. 1995). Such guild designations are not explicitly based on common resource use and abuse the original definition of the guild (SIMBERLOFF & DAYAN 1991). Consequently, the examination of co-occurrences of "guild"

species becomes a moot operation. In this way the useful application of guilds within the conceptual framework within which it was originally formulated is effectively lost.

It should be clear that the classification of species according to characteristics other than common resource use may be most insightful for a variety of ecological and evolutionary questions. Appropriate terms exist for these classifications, such as families (taxonomic similarity), life forms (RAUNKIAER 1934) and alike. Some authors have termed these classifications functional groups. Species of such groups do not necessarily use the same class of resources in a similar way and hence such groups should not be considered guilds (see discussion in SIMBERLOFF & DAYAN 1991). The use of functional groups will be discussed elsewhere (OLFF & DE KROON, in prep.).

(2) Guild membership is not a fixed species trait but is community-dependent

Care should taken to assign species to guilds (FERNÁNDEZ-PALACIOS 1992, BOUTIN & KEDDY 1993, KLIMEŠ et al. 1995), rather than populations of species that co-occur. The guild concept is based on common use of a resource class by populations of different species coexisting in the same community or habitat, i.e. guild species must co-occur sympatrically (ARMBRUSTER 1995). Consequently, the guild should be formulated within a given community; a guild is as much a community characteristic than a species characteristic. An illustrative example is the guild of prairie plants that depends on gopher mounds for their regeneration (PLATT & WEISS 1977). The guild is restricted to a habitat in which gophers are a major disturbance factor. The guild is not confined to the species: it is most unlikely that all the species of this guild depend on gopher mounds for their regeneration in all the habitats throughout their ranges.

A related reason to tie the formulation of guilds to communities, especially for plants, is that plant species often have broad habitat ranges and that they are usually very variable (both genetically and phenotypically) in their resource use. It will depend on the habitat whether or not species will use a common resource, or whether they will use a resource of the same dimension within the common resource class. For example, SNAYDON & BRADSHAW (as cited in FITTER & HAY 1987: 70-71) have shown inter-population differences in the responses to a range of nutrients for *Festuca ovina* and *Trifolium repens* which were related to the nutrient status of the soil on which the populations were collected. *Plantago lanceolata* may predominantly use nitrate in one population but almost exclusively rely on ammonium in another (BLACQUIERE 1986). While it should be encouraged to base the guild classification on characteristics determined under controlled conditions (BOUTIN & KEDDY 1993), the plasticity and genetic variation in the resource use of species should be appreciated.

(3) A guild is associated with a well-defined resource class

In their review of the guild concept, SIMBERLOFF & DAYAN (1991) list as one of the conditions that must be met in order to use the term guild in a fruitful way in research "a clear statement of the criteria and considerations that have led to a particular guild assignment", in which "the role of the foraging method should be emphasized because of its potential importance in effecting differences in resource use". Hence guilds can be designated and guilds assigned to them a priori on the basis of their foraging strategies and the resources that they consume (cf. FOX & BROWN 1993).

Following the conditions of SIMBERLOFF & DAYAN (1991), we have accumulated examples of guilds of plant species in Tab. 1. The species of each of these guilds unambiguously exploit the same class of a resource, as defined above. For example, perennial plant species from mown grasslands are grouped in a single guild because the soil layers in which they root overlap considerably; they can thus be seen to use different resource dimensions within a resource class. Different guilds are recognized among the temperate rainforest species because their leaves exploit the light in very different non-overlapping strata. But, as noted above, the choice of the appropriate resource class and resource dimensions within a class is an a priori decision by the investigator, depending on the questions asked in the study (see also SIMBERLOFF & DAYAN 1991).

Two further notes on resources and the guild assignment. First, species of different guilds use resources of different classes, but these classes usually do not comprise all the resources that affect the life cycle (Fig. 1). Species of different guilds may overlap considerably in the use of other resources than the resource classes that distinguish them. For example, the guilds of rainforest species utilize the light in different strata of the forest, but their roots may overlap considerably and they may use the same soil resources. Second, a resource class may be decomposed in several ways. Soil nutrients may be considered as a resource class consisting of temporal or spatial dimensions, but soil nutrients may also be decomposed in the various minerals such as nitrogen, phosphorus, potassium, etc. Either classification is appropriate, results in the formation of different guilds, and is useful for investigating different mechanisms of resource partitioning within the guild (Tab. 1).

Unfortunately, a number of current studies in plant ecology that apply guilds remain rather vague about the resource class with which the guilds are associated, even if they take differences in resource capture as a basis for their classification. For example, morphological guilds have been proposed, distinguishing grasses and forbs that are assumed to differ in "light-harvesting strategy" (WILSON & ROXBURGH 1994) or morphological/life form guilds such as creeping, rhizomatous, annual and bryophyte guilds reflecting "the importance of soil nutrient capture" (WILSON & GITAY 1995). Given the current knowledge of the ways in which plants forage for light and nutrients (HUTCHINGS & DE KROON 1994, DE KROON & HUTCHINGS 1995) there is no reason to assume that these "guilds" exploit resources in a markedly different way. WILSON & GITAY (1995) admit that their guild classification is based on little more than ignorance (p. 374). Clearly, these guild designations violate the conditions set by SIMBERLOFF & DAYAN (1991), i.e. that guilds should differ in the foraging method and in the resource class that they use. Applying the guild concept in such a superficial way will tell us very little about the underlying processes (such as resource use and competition) that shape the plant community.

(4) Are guilds useful for investigating the importance of resource competition?

One of the most salient points of discussion is whether species of a guild compete more intensively than species belonging to different guilds. There are two classes of opinion that we discuss successively below.

According to the first view, guilds "should be defined independently of the mechanisms by which the members may interact" (SIMBERLOFF & DAYAN 1991: 119; see also MACNALLY 1983) and species should be assigned to guilds a priori on the basis of the resources that they consume (FOX & BROWN 1993). Exploiting the same class of environmental resource in a

Table 1. Some examples of guilds, with their habitat, their resource class and resource dimensions. Examples of resources important in different phases of the cycle are presented (see Fig. 1).

Habitat	Guild(s)	Common resource class(es)	Resource dimension(s)	Reference
Establishment phase				
North American prairie	Wind-dispersed species colonizing badger disturbances	Badger disturbances	● Available soil water ● Distance to nearest disturbance	PLATT & WEISS (1977)
Temperate mown grassland	Forbs with gap-detection mechanisms	Canopy gaps	Light penetrating to the soil surface	OLFF et al. (1994)
Tropical rainforest	● Pioneer tree species ● Canopy tree species	● Large tree-fall gaps ● Small tree-fall gaps and understory	Light availability in the gap	HUBBELL & FOSTER (1987)
Vegetative growth phase				
Temperate mown grassland	Dominant perennial plant species	Soil resources	Nitrogen, phosphorus, water, at different depths in the soil	BERENDSE (1983)
Sand dunes	Winter annuals	Soil resources in winter and early spring	Nutrient and water availability[1]	RATCLIFFE (1961)
Temperate grassland	Herbaceous grassland species	Soil resources	Nitrogen, phosphorus, and other mineral nutrients	TILMAN (1982)
New Zealand temperate rainforest	● Canopy species ● Small trees ● Shrubs ● Forest floor herbs	Light available in each of the strata	Light spectral composition; sunflecks[1]	WILSON (1989)
Reproduction phase				
Eastern North-American mountain grassland	Bumblebee-pollinated flowering plant species	Bumblebees	Densities of different bumblebee species (e.g. short- and long-tongued)	PYKE (1982)
Dispersal phase				
Eastern North-American forest understorey vegetation	*Viola* species dispersed by ants	Seed dispersing ants	Densities of different ant species	CULVER & BEATTIE (1978)

[1]Not investigated in the cited study.

similar way "does **not** mean that guild members do necessarily compete or have necessarily competed: the onus is on ecologists to demonstrate that this is the case." (BEGON et al. 1990: 718; bold as in the original text). Intra-guild competition should not be assumed, for reasons that we have already discussed. First, guild members may use resources of different dimensions which may alleviate competition. Second, if the common resource class is not the limiting resource for population growth rate, competition for that resource may not affect the performance of the species. Other resources that may affect other life cycle transitions may structure the community and the interactions may be equally intense within and between guilds.

A very different opinion is adhered by authors who assume that competition is stronger within than between guilds (PIANKA 1980, VAN DER MAAREL 1988, WILSON 1989). In this view, "guilds would represent arenas of intense interspecific competition, with strong interactions within guilds, but weaker interactions between members of different guilds" (PIANKA 1980). Hence, competition rather than common resource use is taken as a criterium for guild assignment (see also GOLDBERG 1995). It is from this perspective that co-occurrence data of species are examined and guild proportionality (or guild biomass constancy) is interpreted as evidence for intra-guild competition (e.g. WILSON 1989; WILSON & ROXBURGH 1994; KLIMEŠ et al. 1995). The examination of guild proportionality is seen as a **test** of the guild assignment; if the result of the test is negative, the guilds chosen were not the real ones. Wilson and co-workers have taken this one step further by introducing so-called **intrinsic guilds**, groups of species that tend to exclude each other in the real community and that are identified by a statistical optimisation procedure (WILSON & ROXBURGH 1994, WILSON & WHITTAKER 1995). In this approach the a priori designation of guilds on the basis of resource use is abandoned entirely.

In our view, the first opinion discussed above accords with the framework within which guilds were originally formulated. For the sake of conceptual unambiguity as well as for scientific reasons, we would favour the usage of the term guild exclusively within this context. By virtue of the a priori guild structure of communities, we can attempt to link the resource use of species to the complex patterns of species diversity and coexistence. As resource availability may vary markedly between and within communities, and in space and time, resources may be one of the important structuring forces. A priori guild assignments based on resource utilisation, and the co-occurrence data of species of the same guild, may lead to hypotheses regarding the role of competition in structuring plant communities which can be further explored in experimental and modelling studies. Guilds may thus reduce the dimensionality, the degrees of freedom, in plant communities, and this holds both for the species and for the resources involved. This approach is especially promising if guilds are constructed on the basis of the resources that are likely to limit the growth of the populations.

This valuable link between community patterns and resources as a structuring force, operating at the lower (population) level of organisation, is essentially lost following the second opinion, discussed above, where guild membership is equated with negative co-occurrence and competition. This is especially so when guilds are not assigned a priori but post hoc as in the case of Wilson's intrinsic guilds. We would like to stress that the latter approach is an entirely valid and possibly valuable one in studies of community patterns. If non-random patterns emerge, they may be interesting and call for an explanation. However, with others (e.g. BARTHA et al. 1995, LEPŠ 1995) we believe that there are many explanations

possible, and that common resource use and intense competition amongst the species may be just one of them. Denoting these post hoc species groups "guilds" holds the promise that more is known about the species than is actually true (i.e. their resource usage). A more neutral term such as "species assemblages" should be preferred.

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REFERENCES

ARMBRUSTER W.S. (1995): The origins and detection of plant community structure: reproductive versus vegetative process. - Folia Geobot. Phytotax. 30: 483-497.

BARTHA S., CZÁRÁN T. & OBORNY B. (1995): Spatial constraints masking community assembly rules: a simulation study. - Folia Geobot. Phytotax. 30: 471-482.

BEGON M., HARPER J.L. & TOWNSEND C.R. (1990): Ecology. Individuals, populations and communities. - Blackwell Scientific Publication, Oxford.

BERENDSE F. (1983): Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. - J. Ecol. 71: 379-390.

BLACQUIERE T. (1986): Nitrate reduction in the leaves and numbers of nitrifiers in the rhizosphere of *Plantago lanceolata* growing in two contrasting sites. - Pl. & Soil 91: 377-380.

BRAAKHEKKE W.G. (1980): On coexistence: a causal approach to diversity and stability in grassland vegetation. - Agric. Res. Report 902, Pudoc, Wageningen.

BOUTIN C. & KEDDY P.A. (1993): A functional classification of wetland plants. - J. Veg. Sci. 4: 591-600.

CULVER D.C. & BEATTIE A.J. (1978): Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. - J. Ecol. 66: 53-72.

DE KROON H. & HUTCHINGS M.J. (1995): Morphological plasticity in clonal plants - the foraging concept reconsidered. - J. Ecol. 83: 143-152.

FERNÁNDEZ-PALACIOS J.M. (1992): Climatic responses of plant species on Tenerife, The Canary Islands. - J. Veg. Sci. 3: 595-602.

FITTER A.H. & HAY R.K.M. (1987): Environmental physiology of plants. 2nd ed. - Academic Press, London.

FOX J.B. & BROWN J.H. (1993): Assembly rules for functional groups in North American desert rodent communities. - Oikos 67: 358-370.

GILPIN M.E. & DIAMOND J.M. (1984): Are species co-occurrences on islands non-random, and are null hypotheses useful in community ecology? - In: STRONG D.R., SIMBERLOFF D., ABELE L.B. et al. [eds.]: Ecological communities: conceptual issues and the evidence, Princeton University Press, Princeton, pp. 297-315.

GOLDBERG D. (1990): Components of resource competition in plant communities. - In: GRACE J. & TILMAN D.: Perspectives in plant competition, Academic Press, San Diego, pp. 27-50.

GOLDBERG D. (1995): Generating and testing predictions about community structure: which theory is relevant and can it be tested with observational data? - Folia Geobot. Phytotax. 30: 511-518.

GRACE J.B. (1995): On the measurement of plant competition intensity. - Ecology 76: 305-308.

GRACE J. B. & TILMAN D. (1990): Perspectives in plant competition. - Academic Press, San Diego.

GRIME J.P. (1979):. Plant strategies and vegetation processes. - Wiley, Chichester.

HUBBELL S.P. & FOSTER R.B. (1987): The spatial context of regeneration in a neotropical forest. - In: GRAY A.J., CRAWLEY M.J. & EDWARDS P.J. [eds.]: Colonization, succession and stability, Blackwell Scientific Publications, Oxford, pp. 395-412.

HUTCHINGS M.J. & DE KROON H. (1994): Foraging in plants: the role of morphological plasticity in resource acquisition. - Advances Ecol. Res. 25: 159-238.

KLIMEŠ L., JONGEPIER J.W. & JONGEPIEROVÁ I. (1995): Variability in species richness and guild structure in two species-rich grasslands. - Folia Geobot. Phytotax. 30: 243-253.

LAW R. & WATKINSON A.R. (1989): Competition. - In: CHERRETT J.M. [ed.]: Ecological concepts, Blackwell Scientific Publications, Oxford, pp. 243-284.

LEPŠ J. (1995): Variance deficit is not reliable evidence for niche limitation. - Folia Geobot. Phytotax. 30: 455-459.

MACNALLY R.C. (1983): On assessing the significance of interspecific competition to guild structure. - Ecology 64: 1646-1652.

OLFF H., PEGTEL D.M., VAN GROENENDAEL J.M. & BAKKER J.P. (1994): Germination strategies during grassland succession. - J. Ecol. 82: 69-77.

O'BRIEN S.T., HUBBELL S.P., SPIRO P., CONDIT R. & FOSTER R.B. (1995): Diameter, height, crown, and age relationships in eight neotropical tree species. - Ecology 76: 1926-1939.

PIANKA E.R. (1980): Guild structure in desert lizards. - Oikos 35: 194-201.

PIANKA E.R. (1994): Evolutionary Ecology. Ed. 5. - Harper & Collins, New York.

PLATT W.J. & WEIS I.M. (1977): Resource partitioning and competition within a guild of fugitive prairie plants. - Amer. Naturalist 111: 479-513.

PYKE G.H. (1982): Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. - Ecology 63: 555-573.

RATCLIFFE D. (1961): Adaptation to habitat in a group of annual plants. - J. Ecol. 49: 187-201.

RAUNKAIER C. (1934): The life forms of plants and statistical plant geography. - Clarendon Press, Oxford.

ROOT R. (1967): The niche exploitation pattern of the blue-grey gnatcatcher. - Ecol. Monogr. 37: 317-350.

SIMBERLOFF D. & DAYAN T. (1991): The guild concept and the structure of ecological communities. - Annual Rev. Ecol. Syst. 22: 115-143.

STONE L. & ROBERTS A. (1992): Competitive exclusion, or species aggregation. - Oecologia 91: 419-424.

THOMPSON K. (1987): The resource ratio hypothesis and the meaning of competition. - Funct. Ecol. 1: 297-315.

THOMPSON K. & GRIME J.P. (1988): Competition reconsidered: a reply to Tilman. - Funct. Ecol. 2: 114-116.

TILMAN D. (1982): Resource competition and community structure. - Princeton University Press, Princeton.

TILMAN D. (1987): On the meaning of competition and the mechanisms of competitive superiority. - Funct. Ecol. 1: 304-316.

TILMAN D. (1990): Constraints and tradeoffs: toward a predictive theory of competition and succession. - Oikos 58: 3-15.

VAN ANDEL J. & VAN DEN BERGH J.P. (1987): Disturbance of grasslands - Outline of the theme. - In: VAN ANDEL J., BAKKER J.P. & SNAYDON R.W. [eds.]: Disturbance in grasslands, Junk Publishers, Dordrecht, pp. 3-13.

VAN DER MAAREL E. (1988): Floristic diversity and guild structure in the grasslands of Öland's Stora Alvar. - Acta Phytogeogr. Suec. 76: 53-65.

WHITTAKER R.H. (1975): Communities and ecosystems. Ed. 2. - MacMillan, New York.

WILSON J.B. (1989): A null model of guild proportionality, applied to stratification of a New Zealand temperate rain forest. - Oecologia 80: 263-267.

WILSON J.B. & GITAY H. (1995): Limitations to species coexistence: evidence for competition from field observations, using a patch model. - J. Veg. Sci. 6: 369-376.

WILSON J.B., GITAY H., & AGNEW Q. (1987): Does niche limitation exist? - Funct. Ecol. 1: 391-397.

WILSON J.B. & ROXBURGH S.H. (1994): A demonstration of guild-based assembly rules for a plant community, and determination of intrinsic guilds. - Oikos 69: 267-276.

WILSON J.B. & SYKES M.T. (1988): Some tests for niche limitation by examination of species diversity in the Dunedin area, New Zealand. - New Zealand J. Bot. 26: 237-244.

WILSON J.B. & WHITTAKER R.J. (1995): Assembly rules demonstrated in a saltmarsh community. - J. Ecol. 83: 801-807.

ZOBEL K. & ZOBEL M. (1988): A new null hypothesis for measuring the degree of plant community organization. - Vegetatio 75: 17-25.